Social and genetic interactions drive fitness variation in a free-living dolphin population

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Abstract: The evolutionary forces that drive fitness variation in species are of considerable interest. Despite this, the relative importance and interactions of genetic and social factors involved in the evolution of fitness traits in wild mammalian populations are largely unknown. To date, a few studies have demonstrated that fitness might be influenced by either social factors or genes in natural populations, but none have explored howthe combined effect of social and genetic parameters might interact to influence fitness. Drawing from a long-term study of wild bottlenose dolphins in the eastern gulf of Shark Bay,Western Australia, we present a unique approach to understanding these interactions. Our study shows that female calving success depends on both genetic inheritance and social bonds. Moreover, we demonstrate that interactions between social and genetic factors also influence female fitness. Therefore, our study represents a major methodological advance, and provides critical insights into the interplay of genetic and social parameters of fitness.

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Supporting Information

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Table S1. Comparison of four models predicting female Cs (n = 52)

Model	Average effect	SE	t	df	P
$Cs \propto MCs\text{-}_{PA}$		**AIC = 1,920.6**			
$MCs\text{-}_{PA}$	2.25	1.01	2.09	50	**0.035**
$Cs \propto MCs\text{-}_{CR}$		**AIC = 1,927.6**			
$MCs\text{-}_{CR}$	1.89	1.11	1.68	50	0.095
$Cs \propto MCs\text{-}_{PA} + MCS\text{-}_{CR}$		**AIC = 1,907.8**			
$MCs\text{-}_{PA}$	1.99	1.35	1.47	49	0.147
$MCS\text{-}_{CR}$	1.20	1.20	1.00	49	0.320
$Cs \propto MCs\text{-}_{PA} + MCs\text{-}_{CR} + MCs\text{-}_{PA}: MCs\text{-}_{CR}$		**AIC = 1,845**			
$MCs\text{-}_{PA}$	−3.75	2.69	−1.41	48	0.164
$MCs\text{-}_{CR}$	−4.35	2.55	−1.70	48	0.095
$MCs\text{-}_{PA}: MCS\text{-}_{CR}$	38.14	15.43	2.47	48	**0.0171**

GLMM model assumed a binomial distribution and was weighted by number of years for which each female was monitored. Female identity was added as random effect. Explanatory factors are mean Cs of a female's preferred associates ($MCs\text{-}_{PA}$), mean Cs of a female's close relatives ($MCs\text{-}_{CR}$), and their multiplicative interactions ($MCs\text{-}_{PA}: MCs\text{-}_{CR}$). AIC, Akaike information coefficent.

Table S2. GLMM predictors of female Cs (n = 52): Total time spent socializing, relatedness of preferred associates, and home range overlap

Model	Average effect	SE	df	t	P
$Cs \propto M_{HWI} + MR\text{-}_{PA} + HR + M_{HWI}: MR\text{-}_{PA}: HR$					
M_{HWI}	30.23394	25.94688	44	1.165225	0.2502
$MR\text{-}_{PA}$	−9.38067	13.32786	44	−0.70384	0.4852
HR	0.01084	0.01404	44	0.772323	0.4441
$M_{HWI}: MR\text{-}_{PA}$	129.2125	277.6143	44	0.465439	0.6439
M_{HWI}:HR	−0.35773	0.32468	44	−1.10177	0.2766
$MR\text{-}_{PA}$:HR	0.09094	0.19865	44	0.457792	0.6494
$M_{HWI}\ MR\text{-}_{PA}$:HR	−0.81983	3.98184	44	−0.20589	0.8378

A binomial distribution of Cs was assumed. To account for heterogeneity of number of records per female, we weighted the model by the number of years for which each female was monitored. Female identity was added as random effect. The procedure was as for other GLMM models previously described, but with a different set of variables. The explanatory factors are the mean association index to all other females (M_{HWI}), the mean relatedness to preferred associates ($MR\text{-}_{PA}$), the home range size (HR), and their multiplicative interactions.

Table S3. Effect of removal of one individual at a time on significance of both genetic and social pedigree-free animal models

Model	Null LRT Min – Max P values	Const LRT Min – Max P values
Genetic animal model	0.009–0.0461	**<0.001***
Social animal model	0.0202–0.049	**<0.001**†

The possible effect of removal of one individual at a time on significance of both genetic and social pedigree-free animal models was tested by removing one female at a time from the analysis, and measuring new sets of additive genetic and social variances as well as their residuals. Significance of these sets was assessed using both the null model (Null LRT) and constrained model (Const LRT) log-likelihood ratio tests described in *Materials and Methods*. All 51 new sets of analyses were found to be significant for both tests. This indicates that removal of one individual at a time does not change the significance of either the genetic or social animal model.

*Cons LRT-Genetic Effect: Mean − 2× difference in log-likelihood between unconstrained model (our full new models) and constrained model (variance sets to zero) ± SD = 11.58 ± 2.3, mean χ^2_1 = 11.58 ± 2.3, $P < 0.001$.

†Cons LRT-Social Effect: − 2× difference in log-likelihood between unconstrained model (our full model) and constrained model (variance sets to zero) ± SD = 13.2 ± 2.7, meanχ^2_1 = 13.2 ± 2.7, $P < 0.001$.

Table S4. Prebending relatedness matrix for 20 of 52 individuals

No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	1.00	−0.11	−0.11	−0.05	−0.07	−0.01	−0.14	0.07	0.23	0.05	−0.05	−0.05	−0.06	0.08	−0.11	−0.01	−0.14	0.09	−0.02	−0.14
2	−0.11	1.00	−0.03	0.24	0.08	−0.20	−0.30	0.20	−0.01	0.10	0.07	0.42	0.03	−0.38	−0.06	−0.05	0.16	−0.05	0.10	−0.22
3	−0.11	−0.03	1.00	0.05	−0.03	0.16	0.05	0.03	0.25	0.54	0.09	0.14	0.06	0.33	0.12	−0.38	0.27	−0.06	0.20	0.04
4	−0.05	0.24	0.05	1.00	0.40	0.19	0.08	0.09	−0.11	0.24	0.12	0.18	0.07	−0.11	0.06	0.16	0.26	0.05	0.23	−0.11
5	−0.07	0.08	−0.03	0.40	1.00	−0.16	0.02	0.01	0.15	−0.02	0.40	0.28	0.10	−0.08	−0.07	0.04	0.14	−0.08	0.17	0.03
6	−0.01	−0.20	0.16	0.19	−0.16	1.00	0.34	−0.04	0.00	−0.05	−0.15	−0.19	−0.09	0.09	0.26	0.17	0.14	−0.13	0.24	0.32
7	−0.14	−0.30	0.05	0.08	0.02	0.34	1.00	−0.12	0.03	0.11	−0.06	0.22	0.07	0.33	0.13	0.05	−0.13	−0.10	0.09	0.29
8	0.07	0.20	0.03	0.09	0.01	−0.04	−0.12	1.00	−0.01	0.10	0.23	0.14	−0.09	−0.12	0.14	0.10	0.06	0.05	0.25	−0.06
9	0.23	−0.01	0.25	−0.11	0.15	0.00	0.03	−0.01	1.00	0.16	0.04	0.11	0.06	0.27	0.04	−0.31	−0.08	−0.15	0.05	0.03
10	0.05	0.10	0.54	0.24	−0.02	−0.05	0.11	0.10	0.16	1.00	0.09	0.13	0.18	0.16	0.19	−0.13	0.30	0.11	0.11	−0.15
11	−0.05	0.07	0.09	0.12	0.40	−0.15	−0.06	0.23	0.04	0.09	1.00	0.02	−0.22	0.08	0.11	0.05	0.05	−0.12	0.22	−0.11
12	−0.05	0.42	0.14	0.18	0.28	−0.19	0.22	0.14	0.11	0.13	0.02	1.00	0.30	−0.11	0.09	−0.07	−0.04	0.26	0.44	−0.05
13	−0.06	0.03	0.06	0.07	0.10	−0.09	0.07	−0.09	0.06	0.18	−0.22	0.30	1.00	−0.02	−0.06	−0.09	−0.21	0.24	−0.05	−0.01
14	0.08	−0.38	0.33	−0.11	−0.08	0.09	0.33	−0.12	0.27	0.16	0.08	−0.11	−0.02	1.00	0.02	−0.04	−0.09	−0.10	−0.09	−0.09
15	−0.11	−0.06	0.12	0.06	−0.07	0.26	0.13	0.14	0.04	0.19	0.11	0.09	−0.06	0.02	1.00	−0.02	0.02	0.12	0.48	−0.04
16	−0.01	−0.05	−0.38	0.16	0.04	0.17	0.05	0.10	−0.31	−0.13	0.05	−0.07	−0.09	−0.04	−0.02	1.00	−0.12	−0.04	0.12	−0.04
17	−0.14	0.16	0.27	0.26	0.14	0.14	−0.13	0.06	−0.08	0.30	0.05	−0.04	−0.21	−0.09	0.02	−0.12	1.00	−0.16	0.22	−0.12
18	0.09	−0.05	−0.06	0.05	−0.08	−0.13	−0.10	0.05	−0.15	0.11	−0.12	0.26	0.24	−0.10	0.12	−0.04	−0.16	1.00	0.12	0.01
19	−0.02	0.10	0.20	0.23	0.17	0.24	0.09	0.25	0.05	0.11	0.22	0.44	−0.05	−0.09	0.48	0.12	0.22	0.12	1.00	0.02
20	−0.14	−0.22	0.04	−0.11	0.03	0.32	0.29	−0.06	0.03	−0.15	−0.11	−0.05	−0.01	−0.09	−0.04	−0.04	−0.12	0.01	0.02	1.00

For ease of presentation, data for only 20 of the 52 individuals are shown.

Table S5. Postbending relatedness matrix for 20 of 52 individuals

No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	1.00	−0.06	−0.06	−0.03	−0.04	0.00	−0.07	0.04	0.12	0.03	−0.03	−0.02	−0.03	0.04	−0.06	−0.01	−0.08	0.05	−0.01	−0.08
2	−0.06	1.00	−0.02	0.13	0.04	−0.11	−0.16	0.10	0.00	0.05	0.03	0.22	0.02	−0.20	−0.03	−0.03	0.09	−0.03	0.05	−0.12
3	−0.06	−0.02	1.00	0.02	−0.02	0.08	0.03	0.01	0.13	0.28	0.05	0.08	0.03	0.17	0.07	−0.20	0.14	−0.03	0.10	0.02
4	−0.03	0.13	0.02	1.00	0.21	0.10	0.04	0.05	−0.06	0.12	0.06	0.10	0.04	−0.06	0.03	0.09	0.13	0.03	0.12	−0.06
5	−0.04	0.04	−0.02	0.21	1.00	−0.09	0.01	0.01	0.08	−0.01	0.21	0.15	0.05	−0.04	−0.04	0.02	0.08	−0.04	0.09	0.02
6	0.00	−0.11	0.08	0.10	−0.09	1.00	0.18	−0.02	0.00	−0.03	−0.08	−0.10	−0.05	0.05	0.14	0.09	0.07	−0.07	0.13	0.17
7	−0.07	−0.16	0.03	0.04	0.01	0.18	1.00	−0.06	0.02	0.06	−0.03	0.12	0.04	0.18	0.07	0.02	−0.07	−0.05	0.05	0.15
8	0.04	0.10	0.01	0.05	0.01	−0.02	−0.06	1.00	−0.01	0.05	0.12	0.07	−0.05	−0.06	0.07	0.05	0.03	0.03	0.13	−0.03
9	0.12	0.00	0.13	−0.06	0.08	0.00	0.02	−0.01	1.00	0.09	0.02	0.06	0.03	0.14	0.02	−0.16	−0.04	−0.08	0.03	0.02
10	0.03	0.05	0.28	0.12	−0.01	−0.03	0.06	0.05	0.09	1.00	0.05	0.07	0.09	0.08	0.10	−0.07	0.16	0.06	0.06	−0.08
11	−0.03	0.03	0.05	0.06	0.21	−0.08	−0.03	0.12	0.02	0.05	1.00	0.01	−0.11	0.04	0.06	0.03	0.03	−0.06	0.11	−0.06
12	−0.02	0.22	0.08	0.10	0.15	−0.10	0.12	0.07	0.06	0.07	0.01	1.00	0.16	−0.06	0.05	−0.04	−0.02	0.14	0.23	−0.03
13	−0.03	0.02	0.03	0.04	0.05	−0.05	0.04	−0.05	0.03	0.09	−0.11	0.16	1.00	−0.01	−0.03	−0.05	−0.11	0.13	−0.02	−0.01
14	0.04	−0.20	0.17	−0.06	−0.04	0.05	0.18	−0.06	0.14	0.08	0.04	−0.06	−0.01	1.00	0.01	−0.02	−0.05	−0.05	−0.05	−0.05
15	−0.06	−0.03	0.07	0.03	−0.04	0.14	0.07	0.07	0.02	0.10	0.06	0.05	−0.03	0.01	1.00	−0.01	0.01	0.06	0.25	−0.02
16	−0.01	−0.03	−0.20	0.09	0.02	0.09	0.02	0.05	−0.16	−0.07	0.03	−0.04	−0.05	−0.02	−0.01	1.00	−0.07	−0.02	0.06	−0.02
17	−0.08	0.09	0.14	0.13	0.08	0.07	−0.07	0.03	−0.04	0.16	0.03	−0.02	−0.11	−0.05	0.01	−0.07	1.00	−0.08	0.12	−0.06
18	0.05	−0.03	−0.03	0.03	−0.04	−0.07	−0.05	0.03	−0.08	0.06	−0.06	0.14	0.13	−0.05	0.06	−0.02	−0.08	1.00	0.06	0.01
19	−0.01	0.05	0.10	0.12	0.09	0.13	0.05	0.13	0.03	0.06	0.11	0.23	−0.02	−0.05	0.25	0.06	0.12	0.06	1.00	0.01
20	**−0.08**	**−0.12**	**0.02**	**−0.06**	**0.02**	**0.17**	**0.15**	**−0.03**	**0.02**	**−0.08**	**−0.06**	**−0.03**	**−0.01**	**−0.05**	**−0.02**	**−0.02**	**−0.06**	**0.01**	**0.01**	**1.00**

For ease of presentation, data for only 20 of the 52 individuals are shown.